Population dynamics of small mammals in the Drakensberg of Natal, South Africa

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Abstract

Studied two shrews and six rodents which occur in Giant's Castle Game Reserve, a mountainous, predominantly grassland, high rainfall area in South Africa. Sex ratios of all species are given and the population structure cycles of the two most abundantly-trapped animals (*Myosorex varius* and *Rhabdomys pumilio*) are detailed, indicating cycles typical of seasonal breeders and lifespans of 12 to 16 months. Breeding season coincided with the warm wet season (spring and summer). Analyses of the large *M. varius* and *R. pumilio* samples indicated that breeding started about a month later at higher altitudes where temperatures were lower.

Introduction

Population dynamics and reproduction of some of the African small mammals dealt with in this paper have been studied in tropical grassland (Cheeseman and Delany 1979; Delany 1964; Taylor and Green 1976). Perrin (1979; 1980a) studied the rodents *Rhabdomys pumilio* and *Otomys irroratus* in a semi-arid area receiving erratic rainfall, and individual studies on each of these two species were conducted in a South African highveld region (high-lying grassland plains) by Brooks (1974) and Davis and Meester (1981). Prior to this study no published accounts existed concerning the population structure and reproduction of small mammals in an African montane region. In this paper, therefore, we report on the population dynamics of the small mammals which occur in the Drakensberg, the highest mountain range in South Africa.

Study area and methods

This study was conducted in Giant's Castle Game Reserve (GCGR), 29° 08′ to 29° 23′ S and 20° 23′ to 29° 37′ E. The most prominent topographic feature is the Drakensberg escarpment which runs along the western boundary of the reserve at an average altitude of 3000 m, dropping sharply to 2200 m. Below 2200 m the terrain is very broken – numerous rivers flow approximately west to east from the escarpment and have incised steep-sided valleys between which high ridges have remained. GCGR is vegetated mainly by grassland, with limited patches of forest, scrub, and woodland.

The rainfall is seasonal, occurring mainly from October to April (Fig. 1). Mean annual rainfall measured at 1760 m during the study period (1978 to 1980) was 1092 mm which fell on an average of 147 raindays. Rainfall increases with altitude to ca. 1700 to 1800 mm on the escarpment. Snow falls mainly between April and September, but can precipitate during any month above 2500 m. Summers are mild to cool and winters cool to cold (Fig. 1). Temperatures at grass level are considerably lower than those recorded in the Stevenson screen, the mean minimum being below freezing point for five months of the year. Whereas precipitation increases with altitude in the Drakensberg, temperature decreases.

Small mammal sampling was done in all vegetation types between 1500 and 2700 m, using folding aluminium live traps or plywood-based snap traps baited with a mixture of rolled oats and peanut butter.

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Results and discussion

Two shrews (*Myosorex varius* and *Crocidura flavescens*) and six small rodents (*Rhabdomys pumilio*, *Otomys irroratus*, *Dendromus melanotis*, *D. mesomelas*, *Mus minutoides* and *Graphiurus murinus*) were collected. All grassland, scrub, or woodland habitats were dominated by *R. pumilio* or *M. varius*, which contributed 44.1 % and 38.7 % respectively to the total number of small mammals caught. In forest *G. murinus* was dominant.

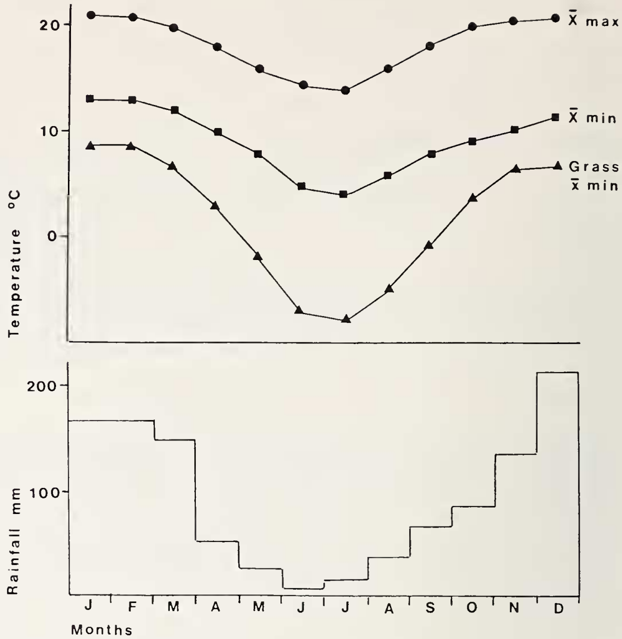


Fig. 1. Mean daily maximum and minimum temperatures, and mean minimum temperature at grass level, recorded at 1860 m in the Drakensberg (Killick 1963), and mean monthly rainfall recorded at 1760 m during the study period

Sex ratios

Sex ratios of trapped small mammals are listed in the table. Deviation from parity was significant only in the two shrew species, in which a preponderance of females was recorded.

Table

Sex ratios of small mammals trapped in GCGR and Chi-square evalution for deviation from parity

Species	Males	Females	Ratio	Chi-square	P
R. pumilio	172	138	1.2 : 1	3.73	NS
M. varius	82	150	0.5 : 1	19.93	< 0.001
O. irroratus	17	16	1.1 : 1	0.03	NS
D. melanotis	14	19	0.7 : 1	0.76	NS
G. murinus	7	11	0.6 : 1	0.89	NS
M. minutoides	8	4	2.0 : 1	1.33	NS
C. flavescens	1	10	0.2 : 1	7.36	< 0.01
D. mesomelas	3	0	–	–	–

NS = P > 0.05

Detailed analyses of data on the two most abundantly-caught species were done to test for significant differences in the sex ratios of adults, sub-adults, snap-trapped and live-trapped animals overall, snap- and live-trapped adults, and snap- and live-trapped sub-adults. No significant departure from a 1 : 1 ratio was observed for any of the different categories of *R. pumilio*. The adult male: female ratio of live-trapped *M. varius* did not differ significantly from parity, but in all other categories there was a significant preponderance of females ($P < 0.05$). Greatest differences were observed amongst sub-adults (Chi-square 14.36; $P < 0.001$) and in the overall snap-trapped sample (Chi-square 12.91; $P < 0.001$).

Brooks (1974) pointed out that trap-based sex ratios do not necessarily reflect the true composition of the population, as they may result from differential trap response or movement patterns. In his study on *R. pumilio* Brooks recorded a non-significant preponderance of males in live-trapped animals but a highly significant 1.7 : 1 ratio in snap-trapped mice, while a significant 0.8 : 1 ratio in favour of females was recorded at birth in a laboratory colony.

The 1.2 : 1 ratio of *R. pumilio* collected in GCGR is similar to the ratios reported by de Wit (1972), Hanney (1965), Perrin (1980a), and Smithers (1971), all of whom recorded a non-significant preponderance of males. The total collection of 435:336 made by Rautenbach (1978) departs significantly from 1 : 1 ($P < 0.01$).

In a study of the activity patterns of the European common shrew *(Sorex araneus)* Vlasák (1980) recorded sexual differences in the activity of immature animals only, but found that males were more active than females. A similar situation may have prevailed amongst *M. varius* in GCGR, but with young females being more active. In at least two other instances (Rautenbach 1976, 1978) females exceeded males in *M. varius* collections, but differences were not significant.

Similar sex ratios to those recorded for two other species collected in GCGR have been reported, viz for *O. irroratus* (Davis 1973; Perrin 1980a, Rautenbach 1978) in which the ratios were ca 1 : 1, and *G. murinus* (Rautenbach 1978; Smithers 1971) in which a preponderance of females was recorded. Rautenbach (1978) and Smithers (1971) recorded ratios in favour of males in *D. melanotis,* but the non-significant departures from parity do not differ greatly from the GCGR ratio which favoured females. Sample sizes of other species collected are too small for consideration.

Population structure

It was possible to examine the population structure of *M. varius* and *R. pumilio* only, as insufficient data were collected on the other species.

The monthly catch of each of the two species was divided into mass classes, using 2 g intervals for *M. varius* and 5 g intervals for *R. pumilio.* The number of animals in each mass

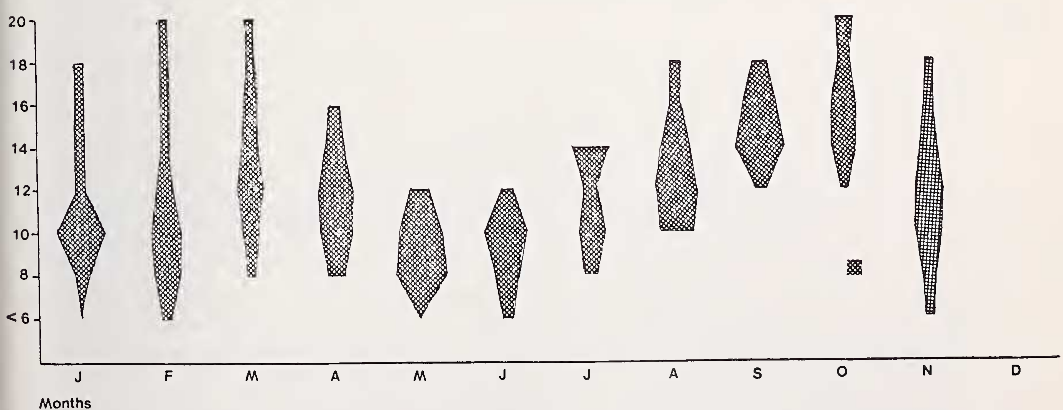


Fig. 2. Mass classes of *M. varius* trapped during each month. The width of the histogram represents the percentage of the total monthly sample which falls into that mass class

class was then expressed as a percentage of the total monthly catch and presented diagrammatically (Figs 2 and 3).

From November to April there was a wide representation of mass classes in the *M. varius* samples, but from May to September fewer mass classes were present. During May and June the catches were made up almost entirely of small animals and no large adults were caught. The pattern strongly suggests that a die-off in adult shrews takes place at the end of the breeding season and that during the next season the population builds up from young animals. From July to September it is obvious that the small May–June animals grow and reach full adult size. The first young animals appear to enter the trappable population in about October.

Baxter (1977) quoted a record of *M. varius* living for as long as two years in captivity, but the GCGR data suggest that under natural conditions most animals survive for only 12 to 16 mo, and that there is a die-off amongst adults by the end of the breeding season.

The population dynamics of *M. varius* have features in common with those previously recorded in some other shrews. It has been shown that European and North American shrews in the wild have a lifespan which does not exceed 18 mo (Vogel 1980). Buckner (1966) found that only 20 % of the new generation of *Sorex cinereus* and *S. arcticus* reached sexual maturity and that almost all surviving animals die before the age of 15 mo. Churchfield (1980) observed similar dynamics in *S. araneus* – 20 to 30 % survived to breed and maximum life expectancy was 13 mo. Generally shrews appear to survive no longer than the end of the breeding season following the one in which they were born.

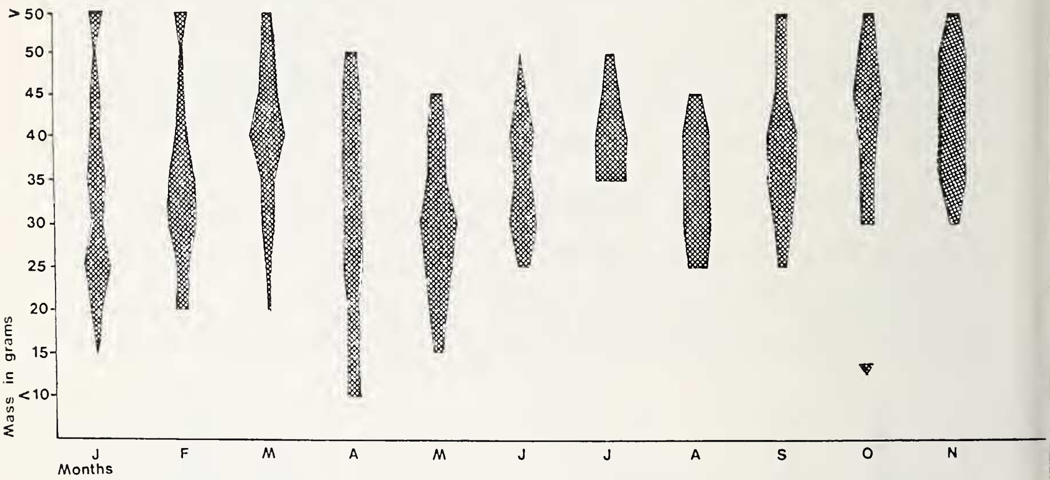


Fig. 3. Mass classes of *R. pumilio* trapped during each month (see *Fig. 2* for explanation)

In the *R. pumilio* samples there was a wide range of mass classes from January to April (Fig. 3). From May to September the catches were made up of what appeared to be some adults and young animals from the previous breeding season. The first young of the season entered the trappable population in October, but no small animals were captured during November. It was mainly during November each year that wet season sampling of the high altitude habitats (2200 to 2700 m) was done, and the absence of young from these samples suggests that at the higher altitudes the breeding season commences later than at the lower altitudes where trapping was done in October (see "Reproduction").

The population structure cycle of *R. pumilio* in GCGR is similar to what Brooks (1974) found near Pretoria and that reported by Perrin (1979) from a study area near Grahamstown, in that the greatest range of age classes was recorded in months following the breeding season, and the smallest range was observed in the non-breeding season, followed by an upward shift in population age structure. PERRIN (1979), working in an area which experiences erratic rainfall, recorded the greatest range of age classes in *R. pumilio* during April and May, following a breeding peak in February. In GCGR the wide size range of animals collected from January to April indicates that the breeding peak occurred earlier and extended over a longer period, probably as a result of the high regular rainfall and the long wet season (see also "Reproduction").

In captivity BROOKS (1974) found that *R. pumilio* had a lifespan which just exceeds two years, but he believed this to be considerably less in the wild, where the oldest individual in his study population was 16 mo old and only 2.3 % of the animals were older than 12 mo. DE WIT (1972) also estimated a similar longevity for *R. pumilio* (17 mo for males and 12 mo for females) but was unable to indicate what proportion of the population lived longer than 12 mo. In the population studied by PERRIN (1979) the age structure suggests that the lifespan exceeds 12 mo in only a small percentage of the mice.

The population structure cycles of *M. varius* and *R. pumilio* are similar in that they exhibit the patterns typical of seasonal breeders. A difference between the two is that a greater range of mass classes was recorded earlier in the season in *M. varius* than was the case in *R. pumilio,* a phenomenon which is related to the onset of breeding at an earlier date in *M. varius* (see also "Reproduction").

Reproduction

Individual species accounts

M. varius

Breeding season in the Drakensberg extended from August to March: pregnant females were collected during these months and lactating females from September to April, and in males an increase in mean testis length was observed in July with a decrease in April (Fig. 4). The percentage of animals in breeding condition (Fig. 4) was highest from September to November (no data for December) and lowest during April to August. Although the percentage of males with inguinal testes examined during August was low there was an increase in mean testis length even in males with abdominal testes.

Mean number of foetuses was 2.8 (N = 19, range 1 to 4).

RAUTENBACH (1978) reported a similar breeding season in the Transvaal where pregnant females were collected from September to March, and similar litter sizes to those from GCGR were recorded by BAXTER and LLOYD (1980): 3.0 in captivity and 2.9 in trapped animals.

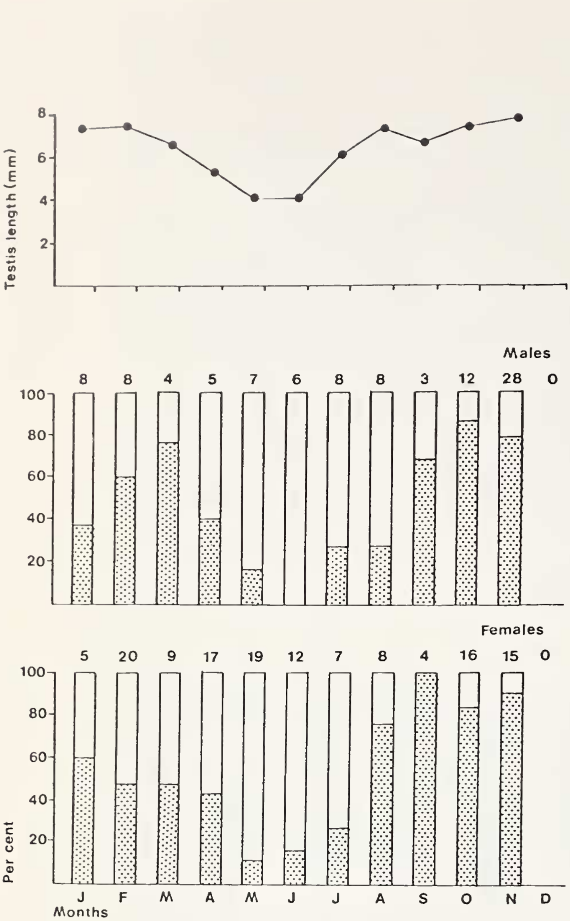
C. flavescens

Pregnant females were collected during October and February. Each of the three pregnant females contained five foetuses. The only adult male collected had abdominal testes during December.

In Uganda DELANY (1964) recorded an average of three foetuses (N = 6, range 2 to 4) in animals trapped just prior to the start of the wet season. BAXTER (1977) observed a breeding season from August to April and a litter size of 3.7 in captive animals.

R. pumilio

Pregnant females were collected during all months from September to March, and no lactating animals were recorded outside this period. Testes began to increase in length during July and decreased during April (Fig. 5). The percentage of animals in breeding condition was lowest from April to June and reached a peak during November (Fig. 5). The data suggest that males become reproductively active about a month earlier than do females. As the breeding season is determined by the female, however, it may be described as extending from August, when mating takes place, to March.



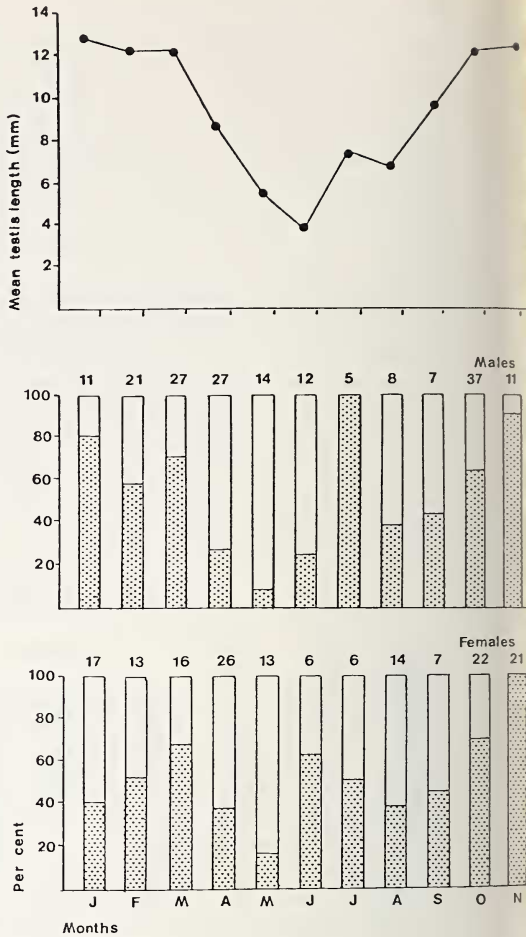


Fig. 4 (left). Reproductive condition of *M. varius,* showing mean testis length (graph), percentage males with inguinal testes and percentage perforate females (shaded bars). Unshaded portions represent males with abdominal testes and imperforate females. Sample sizes are indicated above the bars. – *Fig. 5 (right).* Reproductive condition of *R. pumilio,* showing mean testis length (graph), percentage males with scrotal testes and percentage perforate females (shaded bars) (see *Fig. 4* for explanation)

Mean number of foetuses was 4.6 (N = 22, range 3 to 7).

Breeding in *R. pumilio* appears to coincide with the wet season (Brooks 1974; Hanney 1965; Perrin 1980a; Rautenbach 1978; Taylor and Green 1976), which in GCGR corresponds with the summer months. Smithers (1971) is the only author to report some winter pregnancies in animals collected in an arid region (Botswana). Brooks (1974), Perrin (1980a), and Taylor und Green (1976) found too that males became reproductively active about a month prior to females. The onset of reproductive activity in females usually coincides with the first significant rains of the season (cf. GCGR data, Brooks 1974; Perrin 1980a; Taylor and Green 1976).

Mean litter size has been given as between 4.5 and 5.9 in studies of wild populations (Brooks 1974; de Wit 1972; Hanney 1965; Perrin 1980a; Smithers 1971; Taylor and Green 1976) and 6.5 to 7.0 in captive animals (Brooks 1974; Meester and Hallett 1970).

O. irroratus

Although the sample size is small the data suggest that breeding extended over a longer period than was the case for *R. pumilio:* a lactating female was collected in May, pregnant females were recorded during October, November, and January; and males with scrotal testes were recorded during July, September to November, and January.

Mean number of foetuses was 1.6 (N = 5, range 1 to 2).

Both Davis (1973) and Rautenbach (1978) concluded that *O. irroratus* bred during the warm wet season in the Transvaal, but in the eastern Cape Province Perrin (1980a) found that the species bred throughout the year and that rainfall did not have a significant effect on reproduction. Perrin (1980a) reported a mean litter size of 1.48, which is similar to the mean for the GCGR litters, but the mean litter sizes of 2.3 and 3.2 recorded in the Transvaal by Davis (1973) and Rautenbach (1978) respectively were greater.

D. melanotis

No pregnant females were recorded and the only lactating animal was collected during January. Perforate females were collected during May and November, and males with scrotal testes during April, October, and November. Most immature animals were collected during April and May, which suggests that the young are born during summer.

Very little has been published on the reproduction of *D. melanotis.* Smithers (1971) collected a female containing four foetuses during December in Botswana and recorded pregnancies from December to March in Rhodesia. Delany (1964) recorded a pregnant female with three foetuses during the wet season (July) in Uganda.

D. mesomelas

Males with abdominal testes were collected during September. A lactating female and a male with scrotal testes were recorded during November at Cathedral Peak, 40 km north of GCGR in the Drakensberg (D. T. Rowe-Rowe, unpubl.).

In Malawi Hanney (1965) took two pregnant females at the end of the wet season (March and May) and one at the beginning of the dry season (June). Foetuses numbered two to six.

G. murinus

No pregnant or lactating animals were collected. Perforate females were collected during October and November, and from March to May; males with scrotal testes during September to November; and immature animals during March.

Neither Rautenbach (1978) nor Smithers (1971) recorded any breeding data. Pienaar et al. (1980) reported one pregnant female taken during February. The times at which adults in breeding condition and immature animals were taken in GCGR suggest that this species too breeds during summer.

M. minutoides

As the sample size is small and as no pregnant or lactating animals were collected, interpretation of the data is difficult. Perforate females were collected during May and June, males with scrotal testes during March, October and November, and immature animals during January, August, and October.

Smithers (1971) suggested that the species breeds throughout the year, and in Malawi Hanney (1965) collected pregnant or lactating females during summer, autumn, and winter. The data here presented suggest that breeding occurs throughout the year.

Conclusions

The overall pattern which emerges from the reproductive data collected in GCGR is that most small mammals breed during the wet season. In the Kenya Highlands Taylor and Green (1976) concluded that food was the primary factor regulating rodent reproduction, and rainfall the ultimate factor, by controlling food supply. A similar situation occurred in GCGR. Good rains fell during early spring each year, herbage growth following the rains was rapid, and the nutritional value of the veld (particularly green grass, inflorescences, and forbs) was highest during spring and summer; crude protein content, for example, is as high as 15 % during spring but drops to 2 or 3 % in winter (Scotcher et al. 1980).

A number of other authors have reported small mammal reproduction coinciding with rainfall in regions having a distinct wet season (Brambell and Davis 1941; Chapman et al. 1959; Cheeseman and Delany 1979; Coetzee 1975; Delany 1964; de Wit 1972).

Perrin (1980a) observed a bimodal pattern in the breeding of *R. pumilio,* with a recession in mid-summer, which he positively correlated with the erratic rainfall of the study area. Peaks in the number of births were recorded in February or March, following months of high rainfall. In areas in which rainfall is more predictable and even, *R. pumilio* breeds throughout spring and summer, e.g. in GCGR, study areas near Pretoria (Brooks 1974; de Wit 1972), and in the Kenya Highlands (Taylor and Green 1976).

M. varius reached a breeding peak (Fig. 4) about a month earlier than did *R. pumilio* (Fig. 5). The differences are probably related to the availability of nutritious food: *M. varius* lives entirely on invertebrates (Rowe-Rowe and Meester, in press), high in nutritive value, which might be available earlier in the season than is suitable plant material, which forms the bulk of the diet of *R. pumilio* in GCGR.

Perrin (1980b) reported seasonal changes in the nutrient content of the diet of *R. pumilio.* Breeding in the species followed peaks in nutrient content of the diet. Reproduction of *O. irroratus* in the eastern Cape Province, however, was not influenced by rainfall (Perrin 1980b). The species produces small litters throughout the year (Perrin 1979), and as it lives on large quantities of poor quality herbage during all seasons, Perrin (1980a) concluded that reproduction in *O. irroratus* is not directly dependent on rainfall and food with high nutritive value, and is therefore K-selected (Pianka 1970). *R. pumilio* on the other hand produces large litters seasonally, being dependent on rainfall and nutritious food, and may be considered r-selected.

Brooks (1974) stated that the breeding season of *R. pumilio* was restricted to the wet season, but in considering the factors which controlled reproduction, he rejected rainfall and photoperiod, and stated that only temperature and nutritive value of the diet could be involved – temperature being the most likely factor. I do not see, however, how Brooks (1974) could have completely eliminated rainfall from his consideration, as new growth in plants and seed production (i.e. increase in nutritive value of the food) are dependent on rainfall in the known range of *R. pumilio.*

Data relating to all female *M. varius* and *R. pumilio* collected in GCGR during October and November were examined to see whether there were any differences in the pregnancy rates of animals caught at lower altitudes (< 1900 m) and those trapped at high altitudes (> 2200 m). In *M. varius* (N = 38) 83 % of the low altitude females were pregnant or lactating whereas only 35 % of those from above 2200 m were. Of the *R. pumilio* (N = 35) pregnant or lactating females comprised 45 % of the females collected at low altitudes and a mere 8 % at high altitudes. These percentages not only illustrate the phenomenon that the breeding season starts later at higher altitudes, but further emphasises the conclusion that onset of breeding occurs earlier in the season in *M. varius* than in *R. pumilio.*

Rainfall at the higher altitudes is greater than at the lower altitudes in the Drakensberg (Killick 1963), but temperature decreases with altitude (Killick 1963). The later onset of breeding amongst the two small mammal species at higher altitudes in GCGR is therefore probably due to the effect of lower temperatures.

In considering the findings of Perrin (1980a, b), Brooks (1974) and this study, it appears that rainfall, food, and temperature all play a part in determining the start of the breeding season. Rainfall and food are closely linked, and provided these two factors are present, temperature can further influence the timing of reproduction.

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Zusammenfassung

Populationsdynamik kleiner Säugetiere in den Drakensbergen von Natal, Südafrika

Giant's Castle ist ein in überwiegend grasbewachsenem Bergland mit hohen Niederschlägen gelegenes Wildreservat in Südafrika. Kleinsäuger – zwei Spitzmaus- und sechs Nagerarten – wurden hier über das ganze Jahr verteilt im Höhenbereich zwischen 1500 und 2700 m gesammelt. Für alle acht Arten wird das Geschlechterverhältnis angegeben (Tabelle). Die jahreszeitliche Änderung der Gewichtsstruktur der beiden am häufigsten gesammelten Arten, *Myosorex varius* und *Rhabdomys pumilio* (Abb. 2, 3), lassen auf jahreszeitlich beschränkte Fortpflanzung und eine Lebensdauer von 12 bis 16 Monaten schließen. Auch nach dem Reproduktionszustand der Tiere ist die Fortpflanzung auf Frühjahr und Sommer mit warmer und feuchter Witterung begrenzt. Bei den niedrigeren Temperaturen höherer Lagen setzte die Vermehrung von *Myosorex* und *Rhabdomys* erst ungefähr einen Monat später ein.

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Die Chromosomen von *Microtus arvalis* (Rodentia, Microtinae)

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Abstract

Chromosomal studies in Microtus arvalis (Rodentia, Microtinae)

Studied C- and G-banded karyotypes of *Microtus arvalis* s. str. (2n = 46) from different localities in Europe. Analysis of C-bands revealed large heterochromatic blocks in the centromeric region of several small metacentric autosomes, ranging in numbers from 18 to 22. Further polymorphisms due to pericentric inversions could be demonstrated by G-banding in chromosome pairs nos. 5, 9, 17 and 18. Chromosome homologies with other Microtinae species are discussed.

Einleitung

Die Superspecies „*Microtus arvalis*" umfaßt eine morphologisch ziemlich einheitliche Gruppe mit einem weiten Verbreitungsareal in Europa und Asien (CORBET 1978). Da wegen der geringen Unterschiede morphologische Kriterien zu einer Klassifizierung nicht immer ausreichten, wurden häufig Karyotypanalysen zur Abklärung taxonomischer Probleme herangezogen. Dabei zeigte sich, daß – im Gegensatz zu anderen Merkmalen – die Karyotypen nicht nur zwischen, sondern auch innerhalb der einzelnen Subspecies stark variieren. Während die diploide Chromosomenzahl der asiatischen und osteuropäischen Vertreter zwischen 2n = 46 und 2n = 54 schwankt (SAVIĆ et al. 1971; MALYGIN 1973; MALYGIN und ORLOV 1974; ŽIVKOVIĆ und PETROV 1974; ŽIVKOVIĆ et al. 1974; KRÁL 1976; BELCHEVA et al. 1977), wurden bisher aus Mittel- und Westeuropa nur Formen mit 2n = 46 beschrieben (NIETHAMMER und WINKING 1971; KRÁL et al. 1979) Es waren vor allem die unterschiedliche Chromosomenzahl und Kreuzungsversuche mit sterilen Hybriden, die MEJER et al. (1973) zu einer Abgrenzung der Form mit 2n = 54 als *Microtus subarvalis* von *Microtus arvalis* s. str. veranlaßten.

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